Cambrian monoplacophoran molluscs (Class Helcionelloida)

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Abstract: Cambrian monoplacophoran molluscs (Class Helcionelloida) are morphologically diverse, but also show considerable interspecific variation. While usually small (1-2 mm), they may achieve a size of 30 mm or more. Shell form ranges from low limpets to high cones and these may be straight or curved; coiled shells may be bilaterally symmetrical, dextral or sinistral. This diversity provides a fertile ground for speculation about early molluscan evolution and almost all extant classes of Mollusca have been recognised here. Certainly, molluscs can be traced back to the late Vendian (late Precambrian), but not all classes appeared during the Vendian-Cambrian transition. Small-sized late Vendian-Middle Cambrian molluscs (helcionelloids) show little resemblance to crown molluscan groups, including the living monoplacophorans (tryblidiid Tergomya).

Key Words: Cambrian, Mollusca, monoplacophoran, Helcionelloida, evolution

Most Cambrian monoplacophoran molluscs are morphologically far removed from the familiar present day tryblidiid tergomyan *Neopilina* Lemche, 1957 or its Early Palaeozoic antecedents *Pilina* Koken, 1925 and *Tryblidium* Lindström, 1880. Placed in the Class Helcionelloida, these Cambrian univalves display a variety of shell forms, bearing witness to the first great diversification of molluscs near the Precambrian-Cambrian boundary (Peel, 1991a, b). Indeed, helcionelloids are represented in the first shelly faunas appearing in the late Precambrian in Siberia (Khomentovsky *et al.*, 1990). The helcionelloid shell is typically bilaterally symmetrical (isostrophic), rapidly expanding and coiled through about one whorl, but limpet-like shells, tall cones and strongly laterally compressed morphologies are also conspicuous. *Aldanella* Vostokova, 1962 is a multi-whorled anisostrophic helcionelloid from the earliest Cambrian, seductively reminiscent of the gastropods that first appeared in the latest Cambrian. Anisostrophic shells of *Pelagiella* Matthew, 1895 can be conspicuous throughout the Cambrian and are conveniently placed within the Helcionelloida, even if their precise relationship remains uncertain.

Helcionelloids may be abundant in strata of Early and Middle Cambrian age. A variety of problematic molluscs are known from the Late Cambrian (*e. g.*, Webers *et al.*, 1992) but the helcionelloid record is uncertain. However, we here report undoubted helcionelloids from the latest Cambrian to early Ordovician of Kazakhstan, representing the youngest known members of the class. Thus, the geological record of helcionelloids overlaps with that of the earliest tryblidiid tergomyans such as *Proplina* Kobayashi, 1933 and most other molluscan classes.

Helcionelloids have been interpreted as torted (gastropods, *e. g.* Knight *et al.*, 1960) and un-torted (monoplacophorans) and this latter hypothesis is currently widely supported (Runnegar and Jell, 1976; Peel, 1991a, b; Geyer, 1994; Runnegar, 1996). Their relationship to tergomyans such as *Neopilina* is disputed, with some authors (Runnegar, 1996 and previous works cited therein) uniting all these untorted univalves in a single Class Monoplacophora. Peel (1991a, b; see also Geyer, 1994) reconstructed helcionelloids with the apex at the posterior and the shell expanding anteriorly (endogastric), as distinct from the anterior apex and posteriorly expanding (exogastric) shell of *Neopilina* and other tergomyans. Following the recommendation of Wingstrand (1985) and others, Peel (1991a, b) abandoned Monoplacophora as a formal taxon, employing Class Helcionelloida for the endogastric branch and Class Tergomya for the exogastric trybilidiid stock. Recognition of helcionelloids as the molluscan ancestral group focuses attention in the search for intermediate forms to molluscan classes such as Tergomya, Gastropoda and Cephalopoda to the Late Cambrian. In contrast, the Rostroconchia, as a direct descendant of the Helcionelloida, and the Bivalvia appear to be represented already in the Early Cambrian (Runnegar and Pojeta, 1985).

THE OLDEST MOLLUSCS

Helcionelloids are present in the oldest shelly faunas from Siberia of late Vendian (Nemakit-Daldynian) age

(Khomentovsky *et al.*, 1990; Gubanov and Peel, 1999). These, and the slightly younger, earliest Cambrian, species *Oelandiella korobkovi* Vostokova, 1962 have been referred to the genus *Latouchella* Cobbold, 1921 by most authors, following the unexplained synonymisation of *Oelandiella* Vostokova, 1962 with *Latouchella* by Missarzhevsky (*in* Rozanov *et al.*, 1969; translated into English as Raaben, 1981). Recent re-description of the type materials of both genera by Gubanov and Peel (1998, 1999) has demonstrated that *Oelandiella* is a valid and recognisable genus whereas the widely reported *Latouchella* is uncommon. *Oelandiella* is characterised by comarginal rugae that cross the dorsum whereas the median dorsal area in *Latouchella* is smooth with rugae restricted to the lateral areas. *Latouchella* has also been confused with *Oelandia* Westergård, 1936 from the Middle Cambrian of Sweden, China and Bohemia. The latter genus, however, is not bilaterally symmetrical since the lateral rugae interdigitate at the dorsum (Peel and Yochelson, 1987; Gubanov and Peel, 1998).

Inflated and strongly rugose shells of *Oelandiella korobkovi* occur contemporaneously with the laterally compressed and generally smooth-shelled *Anabarella* Vostokova, 1962, also originally described from northern Siberia. The close relationship between these two genera is demonstrated by the recent description of rugose *Anabarella* from Spain (Vidal *et al.*, 1999). Recently, we have also identified *Anabarella* from the Lontova Formation (Early Cambrian) of Estonia where it occurs together with *Aldanella kunda* (Öpik, 1926) described by Posti (1978).

SIZE, SYMMETRY, AND VARIATION

Most described Cambrian helcionelloids are small, generally 1-2 mm in length (Runnegar and Pojeta, 1985). This reported size range sometimes reflects environmental, preservational and preparational biases because recovery of material suitable for description is commonly accomplished by digestion of phosphatised carbonate rocks in weak acids. Even in the Tommotian (earliest Cambrian), however, there are helcionelloids more than 30 mm long (Dzik, 1991 and personnal observations) (Fig. 1) while undescribed late Early Cambrian material from Sweden can be of similar size. The taxonomic significance of the size differences is uncertain but the importance of considering size in functional morphological interpretations of early molluscs was stressed by Peel (1991b). An unfulfilled need for ontogenetic studies is also apparent in the taxonomy of helcionelloids.

Archaeospira Yu, 1979 from the earliest Cambrian of China closely resembles *Oelandiella korobkovi* (Fig. 2) and the latter name has been applied by earlier authors to material included within the synonymy of the type species *Archaeospira ornata* Yu, 1979 in the detailed re-description given by Qian and Bengtson (1989). They pointed out that *O. korobkovi* is not known to be asymmetrically coiled while the shell of *A. ornata* is slightly sinistral. Furthermore, they commented that a second Chinese species, *Hubeispira nitida* Yu, 1981, is dextral. Gubanov and Peel (1999) noted that some specimens of *O. korobkovi* were slightly dextral but recent study of material from the earliest Cambrian (Tommotian) of the Selinde River, southern Siberia, demonstrates the presence of sinistral, dextral and planispiral bilaterally symmetrical morphs in the same sample of *O. korobkovi*. The sinistral *Archaeospira* may thus prove to be a synonym of *Oelandiella*. The same samples also show dextral morphs of *O. korobkovi* that approach the morphology of the anisostrophic *Aldanella* (Fig. 3). *Aldanella* itself also shows a similar spectrum of

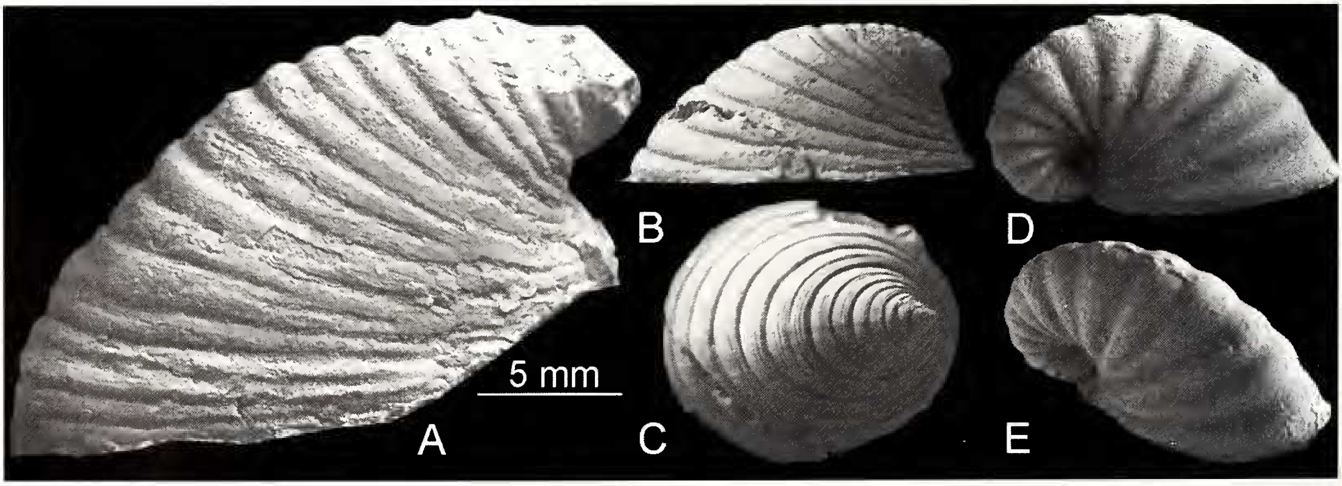

Fig. 1. Large limpet-shaped (A-C) and coiled (D, E) helcionelloid molluscs from the Lower Cambrian (Tommotian, *Dokidocyathus regularis* Zone) of the middle Lena River (southeastern Siberia). **A,** Institute of Palaeobiology, Polish Academy of Sciences, Warsaw (IPB PAN) Ga VIII-3, the largest specimen with broken apex, lateral view. **B, C,** IPB PAN Ga VIII-13, example with well-preserved shell, lateral (B) and apical (C) views. **D, E,** IPB PAN Ga VIII-7, tightly coiled mollusc, lateral (D) and anterio-lateral (E) views.

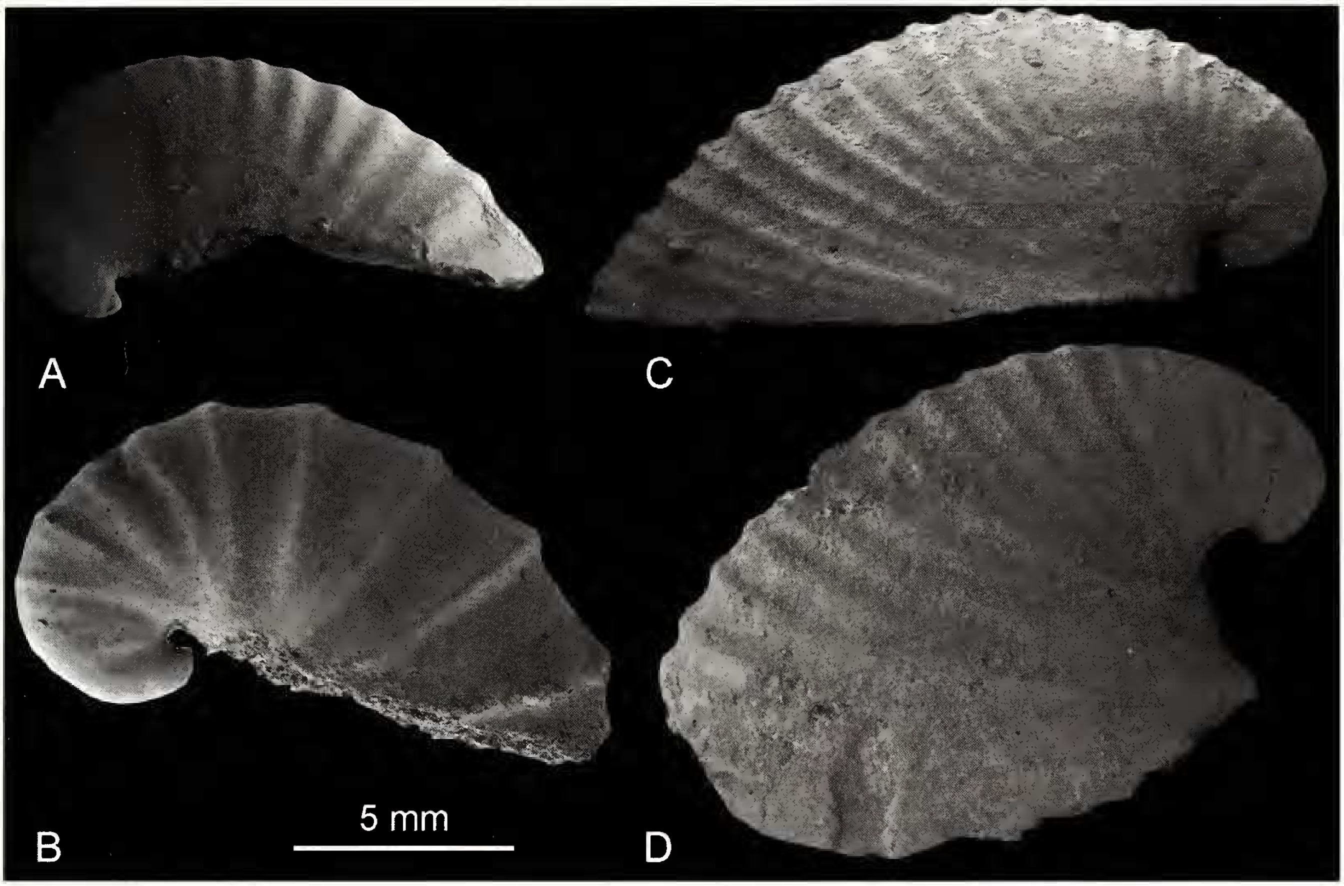

Fig. 2. *Oelandiella korobkovi* Vostokova, 1962 showing variation in comarginal ornamentation and rate of expansion. **A, B,** Museum of Evolution (Palaeontology), Uppsala University (PMU) SIB 1001, 1002, Pestrosvet Formation (early Tommotian) of the Dzhanda River, southeastern Siberia **C, D,** PMU CH 1, 2, Dahai Member (Meisuchunian) of southern China.

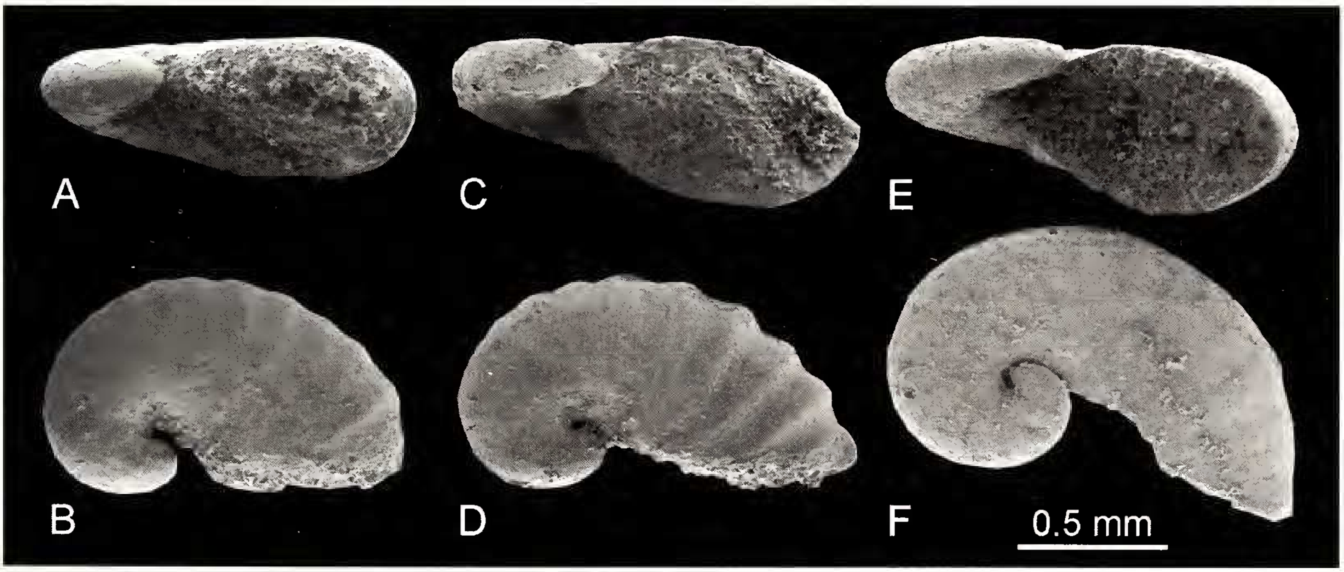

Fig. 3. *Oelandiella korobkovi* Vostokova, 1962 from the lower Cambrian (Tommotian) of the Selinde River, southeastern Siberia. **A, B,** PMU SIB 1003, isostrophic morph in apertural (A) and lateral (apical) (B) views. **C, D,** PMU SIB 1004, dextral morph with comarginal ribs, apertural (C) and apical (D) views. **E, F,** PMU SIB 1005, dextral *Aldanella*-like morph with smooth shell surface, apertural (E) and apical (F) views.

variation occurring within the same sample, and with substantial variation in such characters as rate of whorl expansion, rate of translation along the axis of coiling, tumidity, and tightness of coiling (Fig. 4).

While early Cambrian helcionelloids, including *Aldanella*, appear to be taxonomically diverse, it is now evident from this substantial variation within samples that considerable taxonomic inflation has occurred. Recognition of this variation strengthens interpretation of *Aldanella* as an anisostrophic helcionelloid, refuting suggestions that it could be a gastropod (Runnegar and Pojeta, 1985).

DIVERSITY

Helcionelloids show a remarkable diversity in the Early and Middle Cambrian. The wide aperture and strong comarginal ornamentation suggest that *Oelandiella* was a benthic micro-herbivore or deposit feeder, a mode of life inferred in a variety of other taxa, such as *Latouchella*. Two adaptive morphological trends are clearly visible already in the Tommotian. Expansion of the shell to produce a low cone with a broad to near equidimensional aperture in plan view characterises *Bemella* Missarzhevsky, 1969 and *Helcionella* Grabau and Shimer, 1909, interpreted as benthic deposit feeders adapting to a hardening substratum (Linsley, 1977; Gubanov, 1984). Loss of ornamentation and strong lateral compression in *Anabarella* indicate adaptation to a softer substrate and a semi-infaunal life. This trend from *Oelandiella* to *Anabarella* is continued into *Watsonella* Grabau, 1900 (= *Heraultipegma* Runnegar and Pojeta, 1976), considered to be the oldest member of the Class Rostroconchia Runnegar and Pojeta, 1974 (Pojeta and

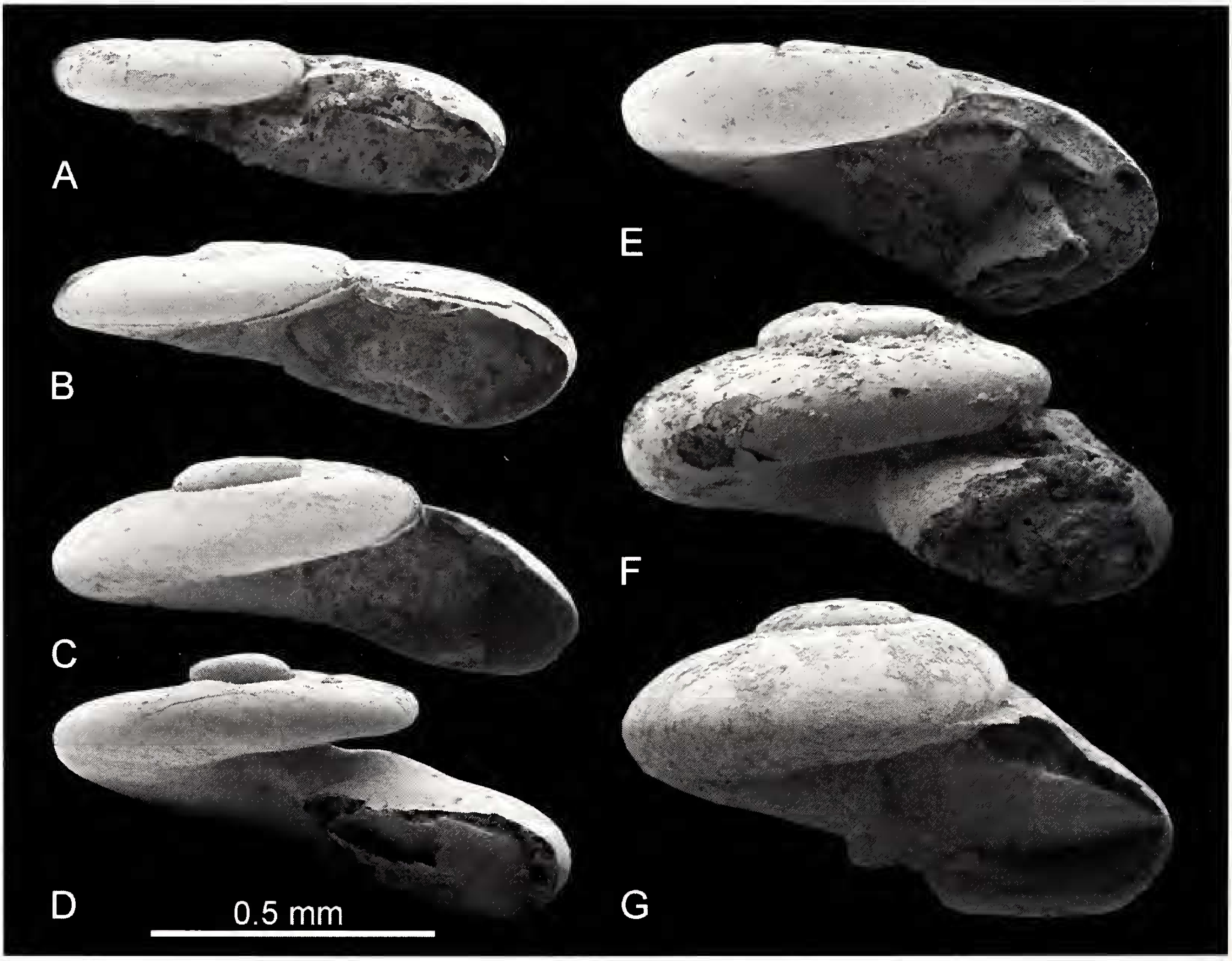

Fig. 4. *Aldanella* sp. from the Lower Cambrian (early Tommotian) of the Anabar River, northeastern Siberia showing the spectrum of shell form variation, PMU SIB 1006-1012, apertural views of all specimens.

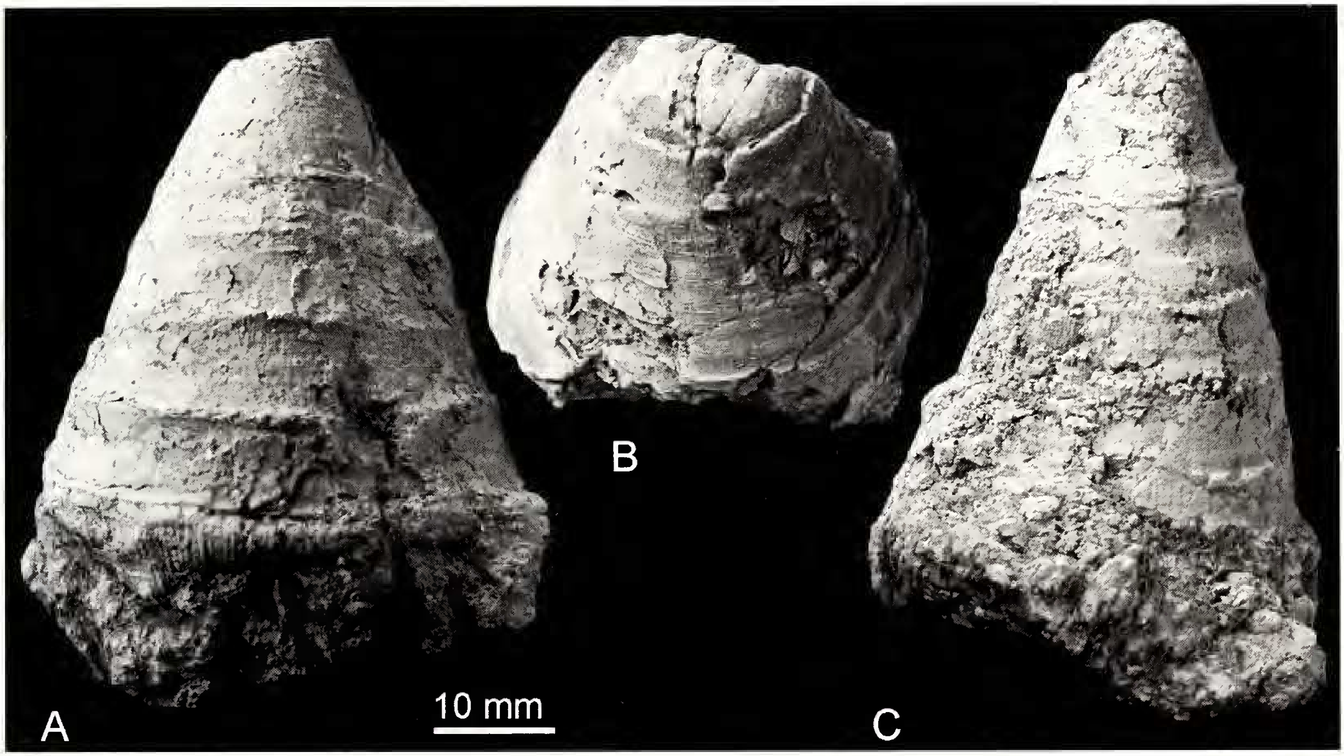

Fig. 5. The hydrothermal vent mollusc *Thermoconus shadlunae* Little, Maslennikov, Morris, and Gubanov, 2000, from the Silurian volcanic rocks of Yaman-Kasy, southern Urals, Russia. **A, C,** lateral views of two specimens in the British Museum of Natural History (BMNH) VF 16 and BMNH VF 18 to show different rates of shell expansion. **B,** paratype, BMNH VF 23, oblique apical view showing the internal septa.

Runnegar, 1976; Runnegar and Pojeta, 1985; Gubanov *et al.*, 1999).

Both of these morphological trends are repeated through the Early and Middle Cambrian (Peel, 1991b). Species referred to *Scenella* Billings, 1872 have widely expanded, limpet-like shells, although these are not universally accepted as molluscs (Yochelson and Gil-Cid, 1984; Landing and Narbonne, 1992). *Marocella* Geyer, 1986 includes several species formerly assigned to *Scenella* (*S. morenensis* Yochelson and Gil-Cid, 1984 and *S. antiqua* Kiaer, 1916), but here, too, there is uncertainty about affinity (Geyer, 1986; Evans, 1992). Morphologically similar shells of uncertain systematic position also occur in the Late Cambrian and Early Ordovician (Stinchcomb, 1986; Webers *et al.*, 1992; Webers and Yochelson, 1999). Lateral compression characterises the Early Cambrian *Stenotheca* Salter, 1859, some species of *Yochelcionella* Runnegar and Pojeta, 1974, and the Middle Cambrian genera *Mellopegma* Runnegar and Jell, 1976 and *Eurekapegma* MacKinnon, 1985. Peel (1991a, b) described a morphological series in the Early-Middle Cambrian *Eotebenna* Runnegar and Jell, 1976 in terms of increased penetration of soft bottom sediments. Culminating in the elongate *Eotebenna viviannae* Peel, 1991, in which convergence of the lateral areas produces separate anterior and posterior openings, this series can be directly compared with morphological adaptations in rostroconchs (Pojeta and Runnegar, 1976; Runnegar and Pojeta, 1985).

THE LAST HELCIONELLOIDS

Recently identified helcionelloids from the earliest Ordovician (Tremadoc) of Kazakhstan are the youngest undoubted members of the class. The specimens are typically helcionelloid in form, coiled through about one whorl. They are about 1-2 mm in length, laterally compressed so that width is about 30 % of length and with ornamentation of comarginal growth lines. The recent recognition of these Kazakhstan helcionelloids requires re-examination of the variety of Late Cambrian-Ordovician problematic isostrophic shells generally placed in the Bellerophontoidea (Gastropoda) or the cyrtonellid Tergomya (Runnegar and Jell, 1976; Peel, 1991b).

A recently described monoplacophoran mollusc from Silurian thermal vent deposits in the Ural Mountains of Russia (Little *et al.*, 1999) provides a challenge to current understanding of tergomyan or helcionelloid evolution.

Thermoconus shadlunae Little, Maslennikov, Morris, and Gubanov, 1999 (Fig. 5) is an unusually large (5-8 cm tall), straight-sided orthoconical shell with a sub-circular cross-section. A specimen with a broken apex reveals internal septa, which are concave towards the aperture (Fig. 5B). The external surface shows two distinct sculpture patterns, with rounded costae in the early stages and reticulate ornamentation with regularly spaced flanges in the late stage.

The shell form of *Thermoconus* is unlike other described tergomyans, but superficially similar tall cones are known in the Late Cambrian-Early Ordovician *Hypseloconus* Berkey, 1898 and *Knightoconus* Yochelson, Flower and Webers, 1973 (Webers *et al.*, 1992). Interpreted as tergomyan, *Thermoconus* represents the first evidence of the migration of this group from the shallow water environments in which it occurs from the Late Cambrian to the Devonian, to the deep-water environments that characterise most of its species at the present day.

While *Thermoconus* is quite reasonably interpreted as a tergomyan mollusc by Little *et al.* (1999), it lacks any muscle scars to substantiate the determination. In addition to their occurrence in the tergomyan *Knightoconus*, septa of the type found in *Thermoconus* are very common in some euomphaloidean gastropods (Gubanov *et al.*, 1995) and among other fossil and recent gastropod taxa (Yochelson *et al.*, 1973). Septation is also a characteristic feature of some helcionelloid molluscs such as *Helcionella chinensis* Walcott, 1905, *H.? insulcata* Rasetti, 1957 and *H. coreanica* Kobayashi, 1958. *Thermoconus* is unlike known Lower Palaeozoic gastropod limpets (*e. g.* Peel and Horny, 1999), but deep water or hydrothermal vent limpets are lacking in the geological record. The array of exotic gastropod limpets described from these habitats at the present day by McLean (1981, 1990) and later papers surely indicates that atypical gastropod limpets could have occurred in vent communities already in the Palaeozoic.

Thermoconus is much larger than any described helcionelloid, but this is a feature of Silurian molluscs in general when compared to their Cambrian progenitors (Runnegar and Pojeta, 1985), although some Tommotian helcionelloid molluscs have already attained a rather large size (see discussion above). Recently one of us (APG) collected possible helcionelloid molluscs, tentatively determined as *Helcionella* sp. with a size up to 8 cm, in the Upper Cambrian-Lower Ordovician Kruzhilikha Formation of the Severnaya Zemlya Archipelago (Arctic Siberia). If we interpret *Thermoconus* as a helcionelloid, it represents a relic of a group of molluscs that were abundant in the Early-Middle Cambrian but survived into the Silurian by taking refuge in the deep ocean. The scenario parallels the more recent history of the Tergomya.

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